

OPINION

Breeding for multi-stress resilience in crops: Myth or possibility?

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HK was supported by the Natural Resources Institute Finland strategic funding (ResiliKasvi) and the Research Council of Finland (Fabagen; funding decision 363375). HK and ICD were supported by a Biotechnology and Biological Sciences Research Council (BBSRC) International Institutional Award (BB/Y514238/1) allowing a legumes workshop at Lancaster, UK.

Social Impact Statement

Climate change threatens millions of farmers worldwide by exposing crops to multiple concurrent or sequential environmental stresses such as drought, heat, waterlogging, and diseases. Although crops have long been selected under naturally occurring multi-stress conditions, breeding pipelines largely focus on optimal or single-stress environments, leaving complex stress combinations under-addressed. Developing crop cultivars that withstand multiple stress scenarios is essential for ensuring food security, food safety, and strengthening farmer resilience. Breeding for multi-stress resilience seems feasible but requires international collaboration among applied crop scientists, pure biologists, and policymakers to develop climate-resilient crops that sustain people and ecosystems.

Summary

Climate change is increasing the frequency and intensity of combined abiotic and biotic stressors that may occur simultaneously or sequentially, dramatically reducing crop growth and yield stability. Plant breeding activities primarily target crop improvement for a single stressor, limiting crop resilience under complex environmental conditions. This opinion paper highlights the complexity of crop breeding for multi-stress growing conditions and discusses major challenges and opportunities to enable plant breeders to develop more climate-resilient crops. It also outlines the importance of integrating conventional breeding approaches with multi-omics and novel breeding technologies to develop multi-stress resilient crop cultivars. Identifying and validating key regulatory genes involved in multi-stress resilience and evaluating their performance across diverse genetic backgrounds, environments, and stress combination scenarios are needed. Although achieving complete multi-stress resilience remains an immense challenge, advances in integrative approaches and cross-disciplinary collaboration are steadily improving the potential to enhance crop resilience to multiple environmental stresses.

KEYWORDS

abiotic and biotic stresses, climate-smart crops, environmental stresses interactions, food security, plant breeding

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1 | INTRODUCTION

Single or multiple abiotic and biotic stressors often challenge crops during their life cycle, reflecting the complex environmental conditions they encounter in the field. Environmental stressors can occur concurrently or sequentially, leading to intricate interactions that further affect crop performance (Raza et al., 2025). Concurrent stresses often trigger interacting physiological responses, whereas sequential stresses can create stress “memory” effects that alter later responses (Alptekin & Kunkowska, 2025). Plant responses to combined environmental stresses are highly interconnected, frequently leading to unique or unpredictable outcomes compared to individual stress response (Zandalinas & Mittler, 2022). Climate change is expected to increase the intensity and frequency of environmental stressors, thereby compromising plant growth and yield potential (Mittler et al., 2025). Developing cultivars capable of withstanding multiple environmental stressors (hereafter multi-stress) is urgently needed to ensure global food security.

Our understanding of plant responses to multi-stress conditions remains limited compared to single-stress scenarios (Pandey & Senthil-Kumar, 2024; Priya et al., 2023), resulting in an incomplete picture of the molecular and physiological mechanisms underlying combined stress response pathways (Cappetta et al., 2020; Husaini, 2022; Jiang et al., 2025). This knowledge is needed to support plant breeders for developing multi-stress resilient cultivars. Knowledge of genes and their underlying mechanisms underpins marker-assisted selection (MAS), genomic selection (GS), and gene transfer technologies, which many plant breeding companies worldwide use as tools to accelerate crop improvement. Breeding for multi-stress resilience refers to crop improvement activities addressing more than one stress factor, which may occur simultaneously or sequentially during the plant's life cycle. National varietal evaluations of yield potential often exclude trials affected by a specific (or multiple) stress. When stresses are considered, most crop breeding programs globally focus on improving cultivar performance for a single-stress, thereby overlooking complex interactions between different temporal combinations of abiotic and biotic stressors (Figure 1). This focus occurs because breeding for even a single stress factor (e.g., drought or some diseases) is already complex. Traits conferring adaptation are quantitative and controlled by numerous small-effect genes. Since the timing and intensity of stresses such as drought at a single site varies from year-to-year (Chenu et al., 2013), breeders likely tailor their selection to conditions that most commonly occur. Traits that may be beneficial under one type of drought scenario (e.g., stomatal closure to conserve water with terminal drought) may compromise productivity under another (e.g., limiting photosynthesis under intermittent drought) with such trade-offs commonplace (Tardieu, 2012). Reproducibly exposing crops to uniform single or multiple stress growing conditions under real-time field conditions remains difficult due to year-to-year variation, particularly when appropriate phenotyping protocols and well-defined traits are lacking. Although breeding programs are generally aware of the environmental stressors affecting their trials, limited resources and the lack of

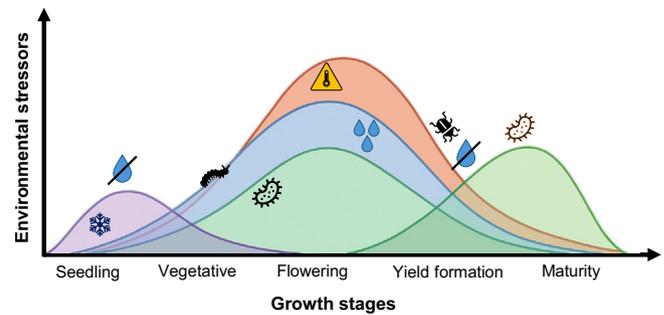


FIGURE 1 Illustrative example showing the complexity of the occurrence of different abiotic (e.g., drought, heat, frost, nutrient starvation, and waterlogging stress) and biotic (e.g., pathogens and insect pests) stress factors (concurrent and sequentially) that crops may experience during their growth and development in field conditions. Note: The combination and sequence of stressors may vary across years, climatic zones, crop species, crop cultivars, and management practices.

methodologies to assess their interactions at multiple scales often constrain understanding of complex multi-stress effects.

As environmental challenges become increasingly variable as the climate changes, breeding for combined abiotic and biotic stress resilience (Burstin et al., 2021; European Commission, 2016; Lecomte et al., 2023) may occupy increasing research attention in the coming years. Growing interest in the plant breeding and research community to move beyond single-stress research toward multi-stress resilience might accelerate crop improvement in this field. Moving in this direction appears inevitable under current and projected climate scenarios. However, breeding for multi-stress resilience remains a major challenge, as breeding for even a single trait remains complex, depending on the crop, number of genes controlling the trait(s) of interest, and the environment. While the significance of environmental stress combinations and stress response mechanisms has been discussed in detail (Cappetta et al., 2020; Muhammad et al., 2025; Pandey & Senthil-Kumar, 2024; Raza et al., 2025), the potential to breed for multi-stress growing conditions has been little explored. This opinion paper highlights key opportunities, limitations, and future considerations for breeding crops resilient to multiple environmental stressors.

2 | HARNESSING GENETIC DIVERSITY FOR MULTI-STRESS RESILIENCE

A successful plant breeding program relies on genetic/allelic diversity of the trait(s) of interest and the extent to which that variation is heritable. Crop genetic resources with resistance or adaptation to abiotic and biotic stressors have already been identified, in tepary bean (high-temperature, drought stresses and resistance to bacterial blight, and seed weevils; Porch et al., 2013), peanut (e.g., resistance to drought, low temperature, and late leaf spot; Upadhyaya et al., 2014), and faba bean (drought–high water use efficiency, chocolate spot, and rust; Khazaei et al., 2018). None of these studies applied concurrent or

simultaneous stresses, assessing germplasm responses from different years in which different stressors, occurred. Relatively few studies evaluated crop germplasm under multiple stress conditions. Crop wild relatives (CWRs) have also shown superior performance under combined or multiple stress conditions (Brozynska et al., 2016), but poor agronomic traits may compromise their productivity. For example, wild tomato relatives harbor alleles for broad abiotic and biotic stress adaptation, but direct introgression can reduce key domestication traits such as fruit size (Khazaei & Madduri, 2022). The linkage drag (Bohra et al., 2022) is likely a major limitation when CWRs are used as donors of multiple genes, requiring multiple generations of backcrossing and selection in aiming to ensure yields are comparable to best-performing elite cultivars. However, new breeding technologies such as CRISPR/Cas9 editing offer opportunities to overcome linkage drag and have already accelerated the manipulation of traits such as tomato fruit size (Yuan et al., 2025). Germplasm with resilience to multiple stress conditions provides pre-breeding material for crop genetic improvement, but trade-offs between multi-stress resilience and yield potential are expected and need to be tested. The genetic architecture underlying multi-stress adaptation in identified germplasm with multi-stress adaptation needs further investigation to support breeding and research programs. For this purpose, diversity sets and mapping populations (bi-parental and multi-parental) need to be developed, genotyped, and phenotyped. This will facilitate gene discovery and cross-species validation of genes involved in multi-stress resilience.

Crossbreeding methods may help develop crop cultivars resilient to multiple stressors. For example, hybrid breeding offers an effective approach by exploiting heterosis to integrate diverse alleles conferring adaptation to various stressors. Thus, hybrid maize cultivars have shown improved tolerance to combined drought and heat stress compared to their parental lines (Cairns et al., 2012; Obata et al., 2015). This genetic diversity often enhances plasticity under variable environments. However, a key limitation is that hybrid breeding is not yet developed or practical for all crop species, particularly those lacking efficient hybridization or seed production systems where efficient hybridization or large-scale hybrid seed production systems remain technically challenging (e.g., rice, barley, faba bean, and common bean). In parallel, gene pyramiding enables the systematic combination of multiple stress-responsive alleles into elite lines, thereby accumulating additive and synergistic effects. Both hybrid breeding and gene pyramiding may accelerate the development of cultivars with broad-spectrum adaptation, supporting sustainable productivity under increasingly complex climatic scenarios. For example, gene pyramiding was used to develop multi-stress (drought + salinity + submergence and submergence + blast) adapted rice cultivars (Muthu et al., 2020; Shin et al., 2022). These approaches require molecular breeding tools to track multi-gene interactions and stability across diverse environments, emphasizing the need for integrative genomics-assisted strategies in future breeding pipelines.

In our view, prioritizing germplasm with demonstrated multi-stress performance rather than single-stress screening should become a routine step in pre-breeding pipelines.

3 | ABIOTIC-BIOTIC STRESS CROSSTALK AND ITS RELEVANCE FOR BREEDING RESILIENT CROPS

Interconnected signaling pathways allow plants to cope with abiotic and biotic stressors, and these responses share extensive molecular overlap (Saijo & Loo, 2020; Suzuki et al., 2014). This crosstalk enables plants to fine-tune defenses, prioritize resource allocation, and maintain growth under combined stress conditions. Understanding the crosstalk between abiotic and biotic stress has important implications for crop improvement under multi-stress growing conditions. Key phytohormones including salicylic acid, jasmonic acid, ethylene, and abscisic acid interact with reactive oxygen species (ROS), calcium fluxes, mitogen-activated protein (MAP) kinase cascades, and transcription factors such as WRKY, NAC, MYB, and basic helix-loop-helix (bHLH) families (Cappetta et al., 2020; Husaini, 2022; Sinha et al., 2025). These shared components allow plants to integrate multiple stress cues and prioritize defense or survival strategies depending on the context. For instance, overexpressing certain NAC or WRKY transcription factors enhances tolerance to drought, flooding, salinity, and pathogen infection (e.g., Chen et al., 2017; Renziehausen et al., 2024; Welner et al., 2016), although multi-stress interactions were not evaluated.

Interconnected signaling networks integrate responses to abiotic and biotic stresses through shared pathways, revealing genetic targets that enhance cross-stress resilience. The plant cell wall functions as a dynamic signaling hub that senses mechanical, chemical, and pathogen cues and coordinates growth-defense trade-offs (Dance, 2025). Light signaling also interacts with other environmental cues such as drought, temperature, and pathogens, influencing how plants balance growth and defense under multiple stresses (Courbier & Pierik, 2019).

In our view, shared regulatory hubs may offer promising entry points for future multi-stress improvement, although their practical use in breeding will require detailed validation across species and environments.

4 | NEW BREEDING TECHNOLOGIES

Advances in gene mapping, transcriptomics, and genome editing tools such as CRISPR/Cas allow identification and manipulation of key regulators underlying crop multi-stress resilience (Karlsson et al., 2024; Razalli et al., 2025; Zhou et al., 2025). Speed breeding, by shortening generation times, complements genomic and gene-editing approaches by allowing faster introgression of alleles conferring resilience to multiple abiotic and biotic stresses into elite cultivars. Understanding the molecular architecture of stress crosstalk is central to breeding resilient crop cultivars. This involves identifying key regulatory hubs that facilitate MAS or GS for combined resistance: pyramiding genes involved in shared signaling pathways to provide durable protection against multiple stresses; integrating multi-omics approaches (e.g., transcriptomics, proteomics, and metabolomics) to uncover genotype-specific responses to combined stresses, and applying genome editing technologies to

precisely modify core regulatory genes. Research in model plant species has greatly advanced our understanding of gene functions and pathways. Translational approaches using these models might accelerate gene discovery for multiple stress conditions, although molecular pathways and gene family members might differ between species due to evolutionary, genetic and physiological differences (Roeder et al., 2025). While this area needs more attention, precise genome editing of WRKY, NAC, and MYB transcription factor genes has enabled the development of plants with enhanced resilience to environmental stresses (Cappetta et al., 2020). For example, knocking out the *GmARM* gene conferred soybean resistance to multiple stressors such as salt-alkali tolerance and *Phytophthora* root rot at seedling stage, without compromising agronomic traits under optimal conditions (Luo et al., 2024). Furthermore, deleting the potato *Parakletos* gene conferred broad-spectrum resistance to multiple pathogens (oomycete, fungi, and bacteria) and enhanced salt and osmotic stress tolerance without affecting plant growth (Zahid et al., 2024). Whether these genome-edited plants provide durable multi-stress resilience under field conditions requires further evaluation, as the literature provides many examples of single genes offering abiotic stress resistance that have not translated from laboratory to the field (Passioura, 2020). Additionally, RNA interference (RNAi) improved crop tolerance to multiple stresses (Saurabh et al., 2014). For example, in maize RNAi used for stress tolerance by combined drought, high light intensity and heat (Simmons et al., 2021). These tools provide a powerful foundation for developing crops resilient to multiple stresses.

Integrating genome editing with genomic-assisted breeding offers realistic pathways to accelerate multi-stress breeding.

5 | PHENOMICS AND TRAIT DISCOVERY FOR MULTI-STRESS SCREENING

Characterizing and identifying plant germplasm with superior adaptation to multiple stress conditions are needed, using high-throughput plant phenotyping platforms that reflect real-time field conditions. Determining how to impose field-relevant combined stress conditions and phenotyping yield-determining traits remains major challenges to breeding crop cultivars adapted to multiple stressors, especially since trade-offs between abiotic and biotic stresses (Figure 2) affect yield potential and stability. New phenotyping protocols should consider both above- and below-ground traits and their inter-relationships. For example, stomatal traits regulate transpiration and gas exchange, thereby influencing abiotic adaptation, and serve as entry points for pathogens, making them important targets for breeding multi-stress resilient crop cultivars (Shapiguzov et al., 2026; Wang & Chang, 2024). Roots similarly contribute to multi-stress resilience by modulating water and nutrient uptake, sensing soil conditions, and interacting with beneficial microbes (Hou et al., 2021) and can regulate stomatal responses via long-distance signaling (Huntenburg et al., 2022). However, our understanding of root-shoot dynamics under combined stress in field conditions remains limited, highlighting a major knowledge gap for multi-stress breeding. High-throughput phenomics, integrating above- and below-ground imaging and sensor-based measurements, offers a powerful tool to capture these interactions in realistic environments, providing actionable data to select multi-stress resilient germplasm.

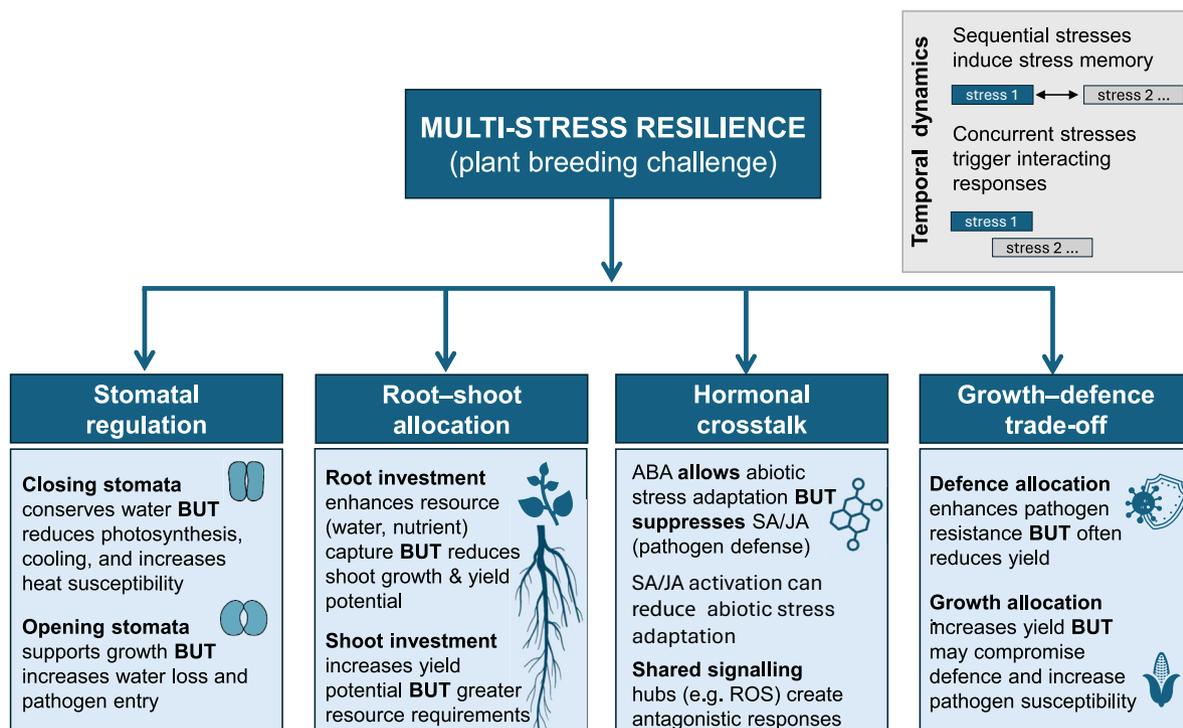


FIGURE 2 Key physiological trade-offs limiting multi-stress resilience in crops. ABA, abscisic acid; JA, jasmonic acid; SA, salicylic acid.

Linking phenotyping with metabolic traits may enhance our understanding of plant adaptation under combined stresses. While proline often accumulates in plant tissues as a biochemical indicator of multi-stress response (Bulut et al., 2025), its contribution to osmotic adjustment is not always assessed and to our knowledge; it has not been used in breeding programs as selecting for high accumulation would discriminate the most stressed plants. Proteomics also provides valuable insights into crop responses to multi-stressors (Haq et al., 2024), highlighting opportunities to integrate metabolic and proteomic data into next-generation phenotyping and selection strategies for multi-stress resilience.

Large-scale, high-throughput multi-stress phenotyping platforms are accessible to only a few institutions, making international cooperation essential to advance research on crop responses to multiple stresses. Coordinated multi-location field trials can exploit natural variation in climate, soils, and stress combinations to generate relevant datasets. Such distributed approaches have been successfully implemented in international breeding programs, for example, through CGIAR (Consultative Group on International Agricultural Research) networks, where standardized protocols, common checks, and shared environmental metadata enable comparative analyses across environments (e.g., Dhondt et al., 2025; Hyman et al., 2017). Harmonizing protocols and sharing data openly among institutions, breeding companies, and farmers will improve access, facilitate meta-analyses, and strengthen multi-stress research.

In our opinion, coordinated multi-location networks represent the most practical near-term solution for generating multi-stress phenotyping data, as high-throughput plant phenotyping investments are beyond the financial means of many national crop improvement programs.

6 | GENOTYPE × ENVIRONMENT × MANAGEMENT

We have limited understanding of how the environment affects plants' responses to multi-stress conditions (multi-stress-adapted genes (G) × environment (E)). When breeding for multi-stress growing conditions, evaluating breeding materials across diverse environmental conditions in multi-site trials is essential (Flavell et al., 2025). Although germplasm may be adapted to both abiotic and biotic stresses, typically selection within specific climatic conditions and stress responses (stable genotypes with low G × E) leaves a major research gap in understanding real-time genetic and physiological mechanisms allowing responses to multiple, simultaneous, or sequential stresses (Robles-Zazueta et al., 2024).

Genotypes by pathogen interactions, including isolate-specific responses, further complicate the prediction of multiple stress impacts across diverse testing environments. This phenomenon is well documented in cereals: Powdery mildew and rust pathosystems in wheat show many examples of isolate-specific R-genes and rapid shifts in virulence that reduce the field durability of single major genes (Kang et al., 2020). Dominant pathogen isolates can change markedly from year-to-year (Kang et al., 2020), and significant variation can also

occur within a single growing season, reflecting dynamic populations even over short time scales (Suffert et al., 2015). Similar genotype-isolate interactions occur in sunflower black stem (Darvishzadeh et al., 2007) and legume root-rot pathosystems (Rubiales et al., 2015), illustrating that pathogen population composition in breeding nurseries can strongly influence apparent genotype performance (Hudson et al., 2024). These patterns often reflect gene-for-gene interactions, where mutations or deletions in pathogen avirulence genes enable evasion of host recognition, leading to rapid loss of previously effective resistance (Dodds, 2025). These complexities motivate testing across multiple pathogen isolates/populations and integrating host and pathogen genomic data into prediction models.

To develop cultivars resilient to multiple stresses, breeders may conduct phenotypic selection in environments that each uniquely represent a specific stress (e.g., heat, salinity, or disease pressure). Identifying genetic materials that perform well across these contrasting environments and intercrossing them for several cycles of recurrent selection accumulates favorable alleles. Subsequently, evaluating the resulting lines through multi-location trials covering all target stresses assesses their stability and combined stress resilience. This approach may allow breeders to effectively combine adaptation to individual stresses into crops that are robust under diverse stress conditions. This approach aligns with the view of Moose et al. (2004) that sustained phenotypic selection and multi-environment evaluation are foundational in crop improvement.

Traditionally, plant breeders have reduced environmental variation in trials by standardizing nutrient and water regimes and pest/disease protection to better estimate genetic effects. In that context, G × E is often treated as experimental “noise” obscuring genetic signals. However, environmental variability and management interactions strongly influence crop performance under multiple stresses conditions. Modern plant breeding practices increasingly aim to characterize and exploit G × E effects (Xu et al., 2022) via multi-environment trials, environmental characterization, GS, crop modeling, and advanced phenotyping. This enables the development of genotypes and management packages suited to diverse and unpredictable production conditions.

Integrating agronomic management practices with plant breeding strategies may enhance crop multi-stress resilience. For example, beneficial soil microbes (e.g., arbuscular mycorrhizal fungi, rhizobia, and plant growth-promoting rhizobacteria) enhance plant tolerance to various environmental stresses (Ahmad et al., 2022; Francioli et al., 2025), while management practices such as deep sowing improve crop drought and heat tolerance (Zhao et al., 2022). Some breeding programs have explicitly selected for traits that improve performance under specific management systems (e.g., high early vigour and improved seedling emergence for unploughed/direct-drill or deep-sowing systems; Watt et al., 2005), but the uptake of selection under distinct agronomic regimes remains limited and merits further integration. Further research is needed, particularly under combined or multiple stress conditions, to study management practices within genotype by stress combination interactions. This approach should enhance our understanding of multi-stress adaptation and improve

the development of crops than can withstand diverse and dynamic field conditions (Le et al. 2025). When targeting multi-stress resilience, particularly at the field scale, management practices must also be considered rather than focusing solely on genetics and breeding. Plant breeding, genomics, and agronomy need to work together to achieve sustainable solutions to withstand combined stress factors.

We recommend that breeders incorporate management-specific selection environments more deliberately when targeting multi-stress resilience.

7 | PREDICTING FUTURE MULTI-STRESS ENVIRONMENTS AND LEVERAGING GLOBAL ANALOGS

Predicting future multi-stress combinations is challenging due to their stochastic nature. Downscaled climate projections and crop simulation models allow probabilistic estimates of stress frequency, intensity, and overlap, especially for major combinations such as heat–drought or drought–disease (Challinor et al., 2014; Hammer et al., 2020). Many regions already experience conditions resembling those projected for other zones, enabling the use of spatial climate analogs. Breeding programs in stress-prone environments have long selected germplasm under natural multi-stress conditions, generating valuable but underutilized datasets (Atlin et al., 2017). Integrating historical trial data, environmental characterization, and climate analogs provides a practical pathway to align current breeding efforts with future multi-stress scenarios without relying solely on predictive models.

8 | MULTI-TRAIT SELECTION INDEX

Breeding crops for multi-stress resilience using a selection index considers combining multiple traits of interest (e.g., yield, drought adaptation and disease resistance) into a single, weighted score for each individual plant. The process defines breeding objectives, records phenotypic and genomic data for various stresses, and calculates an index that ranks individuals, allowing simultaneous selection of the best candidates. After establishing the goals (e.g., improving yield under both drought and low nitrogen), specific traits that contribute to resilience are sought. Compiling data on such traits across diverse germplasm using phenotypic measurements and genomic data allow early selection (before the plants are fully grown) with a formula combining these traits into a single index score. This is typically a linear combination of trait values, each multiplied by a specific weight according to its economic or breeding importance. For example, a single score (or selection index) in plant breeding identifies germplasm combining multiple characteristics such as productivity, resilience, and host plant resistance and produces quality. The index is calculated for each plant within the breeding population, with the highest scores selected for the next cycle because they represent the best combination for target traits. Incorporating this process into the breeding program as a recurrent step over multiple generations can be further enhanced by

using GS, which uses DNA marker data to predict the individual's breeding value, thus accelerating the process. Fine tuning the weights within the index over time ensures consistent progress toward the desired breeding goals.

Multi-trait selection indices integrate multiple stress adaptation and performance traits into a single score to identify superior genotypes, with prominent methods including the multi-trait stability index (MTSI) for environmental stability and the multi-trait genotype ideotype distance index (MGIDI) for distance from an ideal plant (e.g., Debnath et al., 2024; Pour-Aboughadareh et al., 2025). The MTSI evaluates genotype stability and performance across diverse environments and multiple traits by integrating the additive main effect and multiplicative interaction (AMMI) model for dissecting the genotype–environment interaction, and best linear unbiased prediction. Thus, it provides a holistic evaluation of genotype performance by simultaneously considering multiple traits for a single, comprehensive score. The MGIDI facilitates selecting superior genotypes based on their proximity to an ideal genotype across various traits, using principal component analysis (PCA) to organize attributes into components and rank genotypes, thus allowing breeders to select optimal genotypes by weighting different traits and assessing their strengths and weaknesses. These indices assign weights to different traits to reflect their economic or breeding importance, often using statistical techniques like PCA and multivariate analysis to consolidate complex data for more effective, targeted breeding.

The holistic nature of these selection indices might facilitate multi-stress resilience evaluation because stress resilience is a multi-dimensional phenotype rather than a discrete trait, shaped by the interaction of numerous biological factors. Since complex genomic networks rather than a single gene determines ability to withstand environmental pressures, it requires the coordination of multiple physiological systems. For example, MTSI specifically aims to identify genotypes that perform well and remain stable across different growing conditions. Likewise, they bring economic relevance by assigning weights to traits based on their breeding or economic importance, thus ensuring practical and valuable crop selection targets. Efficiency also improves because multiple traits are condensed into a single index simplifying the selection process, making it more efficient than single-trait evaluations. Furthermore, GS and multi-trait indices (e.g., MTSI, MGIDI) within recurrent selection cycles may accelerate to combine complementary resilience traits.

Farmers may have different breeding priorities from those of the professionals managing selection and breeding programs. When farmers help define breeding priorities (participatory breeding), they are more likely to utilize available selection technologies and feel confident in the results (Ceccarelli & Grando, 2007). Hence, employing mixed methods provides a multi-dimensional analysis of farmer-led breeding objectives and their vision for the evolution of the total merit index. Focus groups should explore farmer attitudes toward selection, specifically identifying the drivers and barriers to adoption while gathering input on the design of breeding goals and total merit indices. To scale insights from the focus groups, targeted questionnaires can confirm that these perspectives align with the wider

farming community. The relative weights assigned by farmers to specific trait categories can be directly integrated as coefficients within the selection index. National programs are then equipped to use such a total merit index to select and release cultivars that satisfy end-user demands in specific target environments.

9 | BREEDING STRATEGIES FOR MULTI-STRESS RESILIENCE

Breeding strategies for multi-stress resilience can be broadly grouped into two complementary pathways: phenotype-first, field-driven approaches and gene-first, biotechnology-driven approaches. These pathways differ in their entry points, tools, and types of biological insight generated, but both are required to address complex concurrent and sequential stress combinations (Table 1). The phenotype-first pathway emphasizes selection under naturally occurring stress combinations in multi-environment field trials, whereas the gene-first pathway focuses on mechanistic dissection and targeted manipulation of shared stress-response pathways. Rather than representing competing paradigms, these approaches are complementary and can be iteratively integrated to improve the efficiency and robustness of multi-stress breeding.

10 | CONCLUSIONS AND FUTURE REMARKS

While breeding for multi-stress resilience is not a myth, it is a conditional and context-dependent possibility that has attracted limited attention to date. Breeding for a single stress is already complex, and developing crops resilient to multiple stresses adds another layer of difficulty, making the task seem daunting. However, current climatic conditions highlight the need to develop crop cultivars that can withstand multiple abiotic and biotic stresses throughout their growth cycle. Current improvements in breeding methodologies, multi-omics, agronomic management practices, and new breeding technologies may allow breeding for such complex environments. Despite phenomic and genomic advances, current tools may still not fully capture the complexity of multi-stress interactions, and lack of local resources and infrastructure constrain the implementation of multi-stress breeding programs. Integrating phenotype-first field validation with gene-first discovery, supported by international collaboration, provides a coherent framework for breeding crops resilient to complex stress combinations. Achieving this goal requires close collaboration among pure biologists, plant breeders, crop scientists, statisticians, and other key stakeholders. To date, research on multi-stress resilience has largely utilized controlled growth conditions or specific plant

TABLE 1 Breeding pathways (phenotype- vs. gene-based) for developing multi-stress resilient crop cultivars (*Note: these two approaches are complementary*).

| Dimension | Phenotype-first | Gene-first |
|---|--|--|
| Entry point | Field performance under semi-controlled or naturally occurring multi-stress environments | Molecular dissection of stress responses on identified multi-stress resilience genotype under controlled growing conditions |
| Stress exposure | Concurrent and sequential stresses occurring under realistic, but often uncontrolled, field conditions | Controlled or semi-controlled single and combined stress treatments |
| Typical tool sequence | Multi-environment trials → high-throughput field phenotyping → genotyping → stability analysis → multi-trait indices → recurrent phenotypic selection → GS/MAS | Controlled stress assays → multi-omics profiling → regulatory network analysis → gene mining → genome editing → field validation |
| Genetic architecture captured | Polygenic, context-dependent, small-effect loci | Key regulators and shared signalling hubs |
| Mechanistic insight | Low to moderate | Moderate to high |
| Sensitivity to $G \times E \times M$ | Captured implicitly; depends on environmental characterization | Often underestimated unless explicitly modeled |
| Risk of lab-to-field failure | Moderate | High |
| Suitability for complex stress combinations | High when stress combinations recur naturally | Moderate; depends on accurate reconstruction of stress combinations |
| Main limitation | Environmental noise and slower genetic gain | Context dependence, pleiotropy, translation risk |
| Primary role in modern breeding | Realism, validation, and deployment | Precision, hypothesis testing, and acceleration |
| Scalability across breeding programs | High | Variable; resource- and infrastructure-dependent |

Abbreviations: $G \times E \times M$, genotype \times environment \times management; GS, genomic selection. MAS, marker-assisted selection.

developmental stages. Extending this research to semi-controlled or field conditions is now essential to validate these findings and evaluate how the targeted genes or pathways affect plant performance and yield. Resolving several important unanswered research questions could contribute to this effort, such as the potential role of epigenetics and evolutionary adaptations in shaping plant responses to multiple stressors. Ultimately, realizing multi-stress resilience will depend not only on scientific advances but also on whether breeder attitudes and public/private funding priorities support a meaningful shift toward integrative, multi-stress breeding strategies.

AUTHOR CONTRIBUTIONS

Hamid Khazaei wrote the first draft of the manuscript. Ian Dodd and Rodomiro Ortiz contributed to some sections thereafter, and all authors reviewed the whole manuscript.

ACKNOWLEDGMENTS

We gratefully acknowledge Dr. Pedro Aphalo (University of Helsinki) and Dr. Philippe Monneveux (retired CGIAR scientist) for insightful and valuable comments that helped improve this manuscript. We are grateful to Prof. Herman J. van Eck (Wageningen University) for his valuable insights and constructive guidance, which substantially strengthened the development of this manuscript.

CONFLICT OF INTEREST STATEMENT

The authors declare no competing interests.

DATA AVAILABILITY STATEMENT

No datasets were generated or analyzed during the current study.

ETHICS STATEMENT

As this is an opinion article, no ethics approval is required.

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How to cite this article: Khazaei, H., Dodd, I. C., & Ortiz, R. (2026). Breeding for multi-stress resilience in crops: Myth or possibility? *Plants, People, Planet*, 1–10. <https://doi.org/10.1002/ppp3.70185>